PROVENANCE DOES MATTER: LINKS BETWEEN WINTER TROPHIC SEGREGATION AND THE MIGRATORY ORIGINS OF EUROPEAN ROBINS

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Abstract.

Amongst migratory species, it is common to find individuals from different populations or geographical origins sharing staging or wintering areas. Given their differing life histories, ecological theory would predict that the different groups of individuals should exhibit some level of niche segregation. This has rarely been investigated because of the difficulty in assigning migrating individuals to breeding areas. Here, we start by documenting a broad geographical gradient of hydrogen isotopes (δ^2H) in robin *Erithacus rubecula* feathers across Europe. We then use δ^2H, as well as wing-tip shape, as surrogates for broad migratory origin of birds wintering in Iberia, to investigate the ecological segregation of populations. Wintering robins of different sexes, ages and body sizes are known to segregate between habitats in Iberia. This has been attributed to the despotic exclusion of inferior competitors from the best patches by dominant individuals. We find no segregation between habitats in relation to δ^2H in feathers, or to wing-tip shape, which suggests that no major asymmetries in competitive ability exist between migrant robins of different origins. Trophic level (inferred from nitrogen isotopes in blood) correlated both with δ^2H in feathers and with wing-tip shape, showing that individuals from different geographic origins display a degree of ecological segregation in shared winter quarters. Isotopic mixing models indicate that wintering birds originating from more northerly populations consume more invertebrates. Our multi-scale study suggests that trophic-niche segregation may result from specializations (arising in the population-specific breeding areas) that are transported by the migrants into the shared wintering grounds.

Keywords: Seasonal matching, ecological segregation, *Erithacus rubecula*, migration, stable isotopes

INTRODUCTION

Billions of migratory birds, as well as countless other animals, seasonally shift positions across vast geographical areas. At the end of the migratory journey, they often face numerous conspecific competitors from diverse geographical origins that share common non-breeding quarters (Block et al 2005, Newton 2008, Blumenthal et al 2009). The degree of population overlap and competition in the non-breeding season may have varied implications, from demographic regulation to the evolution and shaping of migratory systems (Rickleffs 1992, Bell 2005), but because of difficulties in assigning individuals to different origins, thus far virtually nothing is known of the ways individuals from different populations of the same species coexist.

There are theoretical reasons to expect segregation and ecological differentiation when multiple populations locally coexist. For example, local adaptations or specializations associated with the breeding grounds in different latitudes and habitats (Peterson 1993) may well be transported to wintering sites by migrating individuals (Price & Gross 2005, Rayner et al. 2011). Alternatively, competitive asymmetries on the wintering grounds may force habitat/trophic segregation of different populations where resources are limited (Fretwell & Lucas 1970, Greenberg 1986). For example, if some migrants arrive earlier, they may gain advantage from earlier ownership of non-breeding territories and win more territorial contests against later arrivals (Tobias 1997). In this scenario, populations at disadvantage may have no alternative but occupying different niches (Greenberg et al. 2001), perhaps with time adapting to them. Asymmetries may also occur due to carry-over effects (Catry et al. 2013) and matching of habitat quality between breeding and wintering sites has also been reported for non-territorial migrants (Gunnarsson et al. 2005).

In species such as European robins *Erithacus rubecula* (hereafter "robins") and in blackcaps *Sylvia atricapilla*, sedentary Iberian populations mostly occupy woodland habitats where they also nest, whereas migrants predominate at shrubland sites where no breeding takes place (Pérez-Tris & Tellería 2002, Tellería & Pérez-Tris 2004). It is unclear whether such segregation results from the predominance of sedentary individuals at sites where they hold year-round territories (Campos et al. 2011a), or whether there is a difference in winter habitat choice irrespective of its potential value for future reproduction. A recent study suggests that amongst migratory blackcaps there is no difference in the habitat distribution of birds of different origins (de la Hera et al. 2012). However, segregation may also occur at finer ecological scales, such as among micro-habitats or dietary preferences.

In this paper, we use robins as a model species to determine whether there is an ecological segregation of wintering migratory individuals of different geographical origins at multiple ecological scales. We used stable hydrogen isotope ratios (δ^2H) in robin feathers to give an indication of geographic origin, as these ratios in amount-weighted mean annual precipitation occur in a pronounced gradient across Europe along a southwest-northeast axis (Hobson et al. 2004). This is the main direction of migration of robins occurring in western Iberia (Bueno 1998). We also use stable carbon and nitrogen isotope ratios and multiple source mixing models to assess differences in diet (Inger & Bearhop 2007, Parnell *et al* 2010). Specifically we investigate the question at three hierarchical spatial scales plus at one further ecological dimension: (1) regional, by comparing different sectors of Iberia; (2) macro-habitat, by comparing two contrasting habitats in the same region; (3) micro-habitat, by making detailed habitat measurement within two study sites; and (4) diet, as assessed through stable-nitrogen isotope ratios in blood, a proxy for trophic level.

METHODS

Study species

European robins are small passerines common across almost the entire continent. Northern and eastern populations are fully migratory, while at the western and southern edge of the range (including much of Iberia) they are mostly sedentary. At mid-latitudes, robins are partial migrants (Cramp 1988). In western Iberia, robins are extremely common winter visitors, occupying virtually every type of habitat with some tree or shrub cover, feeding on invertebrates, berries, olives and acorns (Herrera 1977, 1998). Some individuals defend winter territories while others behave as floaters (Cuadrado 1997).

Feather sampling across Europe

Because feathers, once fully developed, are metabolically inert, they reflect the environment in which they were grown. Flight feathers of robins <1 year old are grown in the nest. Adult feathers are moulted after reproduction, while birds are still on the breeding grounds (Cramp 1988). Note that robins are highly faithful to nesting areas and breeding dispersal, when it occurs, is mostly of less than 10km (Paradis et al. 1998). We sampled robin feathers grown in 2007 across multiple European locations in Portugal, France, Sweden and Russia. Stable isotope ratios in terrestrial ecosystems are known to show site-specific variations that are superimposed on broad geographical trends (Wunder et al. 2005). Hence, to avoid obtaining spurious results caused by local variation, within each region/country we tried, as much as possible, to sample individuals from as many different locations (covering a broad range of latitudes) as possible. Adult robins were sampled during the 2008 breeding season in Portugal (16 sites from north to

115 south; late April to mid July), France (10 sites, from north to centre, late May to early July) and
116 Russia (2 sites, Kaliningrad enclave, Baltic region, late May and June). Scandinavian robins
117 were sampled during migration at the southern tip of Sweden, at Falsterbo (55º 23' N, 12º 50' E),
118 where migrant robins originating from all over Sweden and (less so) from Finland occur during
119 autumn (Karlsson et al. 1988). Trapping took place on 5 different dates, from mid September to
120 mid-October 2007, covering the main migratory period. It is therefore likely that each of the 36
121 individuals sampled here came from a different breeding site. Note that individuals sampled in
122 autumn 2007 and adults sampled in spring 2008 would have all grown their feathers in the same
123 breeding season.
124 Each sampled robin was ringed. The innermost secondary was cut and preserved for
125 isotope analysis. This feather was chosen as it is rarely lost by accident, which prevents the
126 unintended sampling of replacement feathers grown away from the breeding site.
127
128 *Winter sampling in Iberia*
129 Robins were captured using mist-nets and baited traps during the winter (from mid-November
130 2008 to mid-February 2009) at 5 locations, covering the full wintering range along a NE-SW
131 axis on the western part of Iberia: (1) Irun, Northern Spain (43º20'N, 1º 47'W) in mostly
132 woodland habitats (10m altitude; N = 22 robins); (2) Salvaterra do Extremo, Central Portugal
133 (39º 52'N, 06º 54' W) in open cork oak woodland (350m altitude; N = 12 robins); (3) Charneca
134 (near Alcochete), Central/South Portugal (38º 49'N, 08º 49' W) in open cork oak woodland with
135 virtually no undergrowth (25m altitude; N = 45 robins); (4) Arrábida, Central/South Portugal
136 (38º 27'N, 09º 01' W) in Mediterranean shrubland (200m altitude; N = 77 robins); (5) Charito,
137 Algarve, South Portugal (37º10'N, 08º 27'W), in an open mixture of woodland/shrubland with

carob trees, mastic and olive trees (50m altitude; N = 17 robins). Robins do not nest at any of the sites where traps or nets were placed.

Sites 3 and 4 are separated by just 45km and have a similar climate. They were selected to represent the greatest possible contrast in terms of shrub and tree cover, as these variables are known to influence the distribution of robin of different age, sex and size classes (Tellería *et al*. 2001, Catry *et al*. 2004, own unpubl. data). Within these main study sites (sites 3 & 4), robins were trapped with spring traps baited with mealworms only, to ensure they were foraging at the site of capture, and not just commuting to another place. At each exact capture location (and following Catry *et al*. 2004) we visually estimated the following micro-habitat variables, in a radius of 20m around the trap: a) mean canopy height, b) percentage canopy cover, c) mean height of the shrub layer (shrubs were defined as woody plants less than 3 m tall), d) percentage shrub cover, e) percentage bare ground or short-grass (< 10 cm tall) cover and f) percentage long-grass cover.

Robins captured in winter were aged according to Svensson (1992) and processed in the same way as described above for spring. Additionally, for birds captured at Charneca and Arrábida, we measured each of the 9 primaries using a ruler with a pin. Pectoral muscle profiles were scored with reference to the prominence of the sternal keel and muscle shape, on a 4-point scale following Bairlein (1995; see also Gosler, 1991).

Approximately 60 µl of blood were obtained by puncturing the *vena ulnaris*. A drop was preserved in ethanol for molecular sexing and the remaining was frozen until further processing. Sexing was done through the amplification by PCR (polymerase chain reaction) of a fragment of the CHD gene, using the primers P2 and P8 (Griffiths *et al*. 1998).

160 At Charneca and Arrábida, samples of the most common invertebrates, berries and acorns
161 likely to be part of robin diet (Herrera 1977, 1998, Debusse & Isenmann 1985) were collected
162 during winter and frozen for subsequent laboratory analysis.
163
164 *Stable isotopes*
165 i) Hydrogen isotopes
166 The sampled feathers from our study birds were carefully washed in distilled water and oven
167 dried and left for a week equilibrating. Feathers were then cut very finely and weighed into silver
168 cups and loaded into a zero-blank autosampler ready for analysis by continuous flow isotope
169 ratio mass spectrometry (CF-IRMS), using a high temperature reduction system (TC/EA)
170 interfaced with a Thermo-Fisher-Scientific Delta V Plus IRMS. We used the "comparative
171 equilibration" (Wassenaar and Hobson, 2003) approach to correct the δ^2H isotope data, Briefly,
172 the steam equilibration takes place in a modified Costech zero-blank autosampler containing
173 keratin standards. Water of known δ^2H_{VSMOW} (W64444, d2H=-399.1‰, provided by USGS-
174 RSIL; or alternatively S9, an internal water standard, δ^2H_{VSMOW} = +99.09‰) is injected into the
175 evacuated hot autosampler in a 110°C oven. Following equilibration, evacuation and cooling to
176 room temperature the autosampler is reattached to the TC/EA, purged with helium gas and run as
177 normal. Non-exchangeable standards are used to correct raw hydrogen isotope data; these were
178 IAEA-CH7 (polyethylene foil, δ^2H_{VSMOW} = -100.3‰), C36 (hexatriacontane provided by A.
179 Schimmelmann, δ^2H_{VSMOW} =246.7‰) and an internal polythene foil standard "BOS" (δ^2H_{VSMOW}
180 = -82.1‰). Two runs using the two widely disparate water standards above, allows %H
181 exchangeability and unexchangeable δ^2H_{VSMOW} to be calculated. As such that the δ^2H data here
182 represent the unexchangeable hydrogen and fixed to the VSMOW-VSLAP scale.

The standards used for this approach are CFS (chicken feathers; δ^2H_{VSMOW} = -147 ± 5 ‰, Hobson and Wassenaar 2008), BWB-II (bowhead whale baleen; δ^2H_{VSMOW} = -108 ± 4 ‰, Hobson and Wassenaar 2008) and ISB (Icelandic black-legged kittiwake, *Rissa tridactyla* feathers δ^2H_{VSMOW} = -72 ± 3 ‰, Fox et al. 2007). A fourth keratin standard WG (Willow grouse *Lagopus lagopus* feathers, δ^2H_{VSMOW} = -135 ± 1 ‰, unpublished data) is run independently of the calibration (see also Evans et al. 2012). All four standards were run in triplicate in five measurement runs; collectively the fifteen WG standards had a δ^2H_{VSMOW} of -135.38 ± 2.89‰. All δ^2H values quoted are non-exchangeable hydrogen derived from the comparative steam equilibration technique.

ii) Carbon and nitrogen isotopes

Whole blood, whole insects, berries and acorns were oven dried, reduced to a homogeneous powder, and weighed into tin cups then also analysed for nitrogen ($\delta^{15}N_{AIR}$) and carbon ($\delta^{13}C_{V\text{-}PDB}$) isotope ratios by CF-IRMS, using a Costech ECS 4010 elemental analyser connected to a Thermo-Fisher-Scientific Delta XP Plus IRMS. Internal laboratory standards included gelatin, and two alanine standards spiked with ^{13}C- and ^{15}N-enriched alanine respectively. These internal standards are checked monthly against international reference materials USGS 40 and USGS 41 (glutamic acid), IAEA N1, N2 and USGS25 (ammonium sulphate) and IAEA CH6 (sucrose). Repeated (>20) $\delta^{15}N$ and $\delta^{13}C$ measurements in each run gave standard deviations of ~0.2 and 0.1‰ respectively.

All the analyses were performed at the same laboratory of the NERC Life Sciences Mass Spectrometry Facility at East Kilbride, Scotland.

Statistical analysis

206 An index of shrub volume at each trapping location was obtained by multiplying shrub cover by
207 its mean height. This micro-habitat variable has been shown to contribute to predict size, age and
208 sex-ratios of captured robins in winter (Catry et al. 2004).
209 Bird populations with a greater migratory tendency tend to have longer and more pointed
210 wings, and this general pattern applies to robins, with more northerly populations differing from
211 southern and predominantly sedentary ones (Pérez-Tris *et al*. 2000, Tellería *et al*. 2001). Hence,
212 using the measurements of individual primary feathers, we calculated a wingtip pointedness
213 index (C_2) derived from Size-Corrected Components Analysis - SCCA (Lockwood *et al.* 1998).
214 This was only done for robins wintering at Charneca and Arrábida, as most other samples had
215 been collected by collaborators who were unable to provide measurements of primary feathers.
216 In order to estimate the contribution of each prey type in the diet of individual robins, we
217 developed an isotopic mixing model in the "R" package SIAR (Parnell et al. 2010, R
218 Development Core Team 2012). The procedure implements a Markov Chain Monte Carlo
219 algorithm to seek likely combination of prey contributions that best match the isotopic signature
220 of the consumer, taking into account tissue- and species-specific discrimination factors of dietary
221 items. Natural variability in isotopic signature of food sources and in trophic discrimination is
222 dealt with within the Bayesian approach implemented by SIAR (Parnell *et al*. 2010). Prey items
223 were aggregated according to prior knowledge of their feeding habits in the regions and included
224 four major types: Ants, other insects, *Quercus sp.* acorns and berries, the latter only present in
225 one of the sites (Arrábida). Trophic enrichment factors were set at 1.7±0.17‰ and 2.4±0.24‰
226 and for carbon and nitrogen respectively (Hobson and Bairlein 2003).
227 We used general linear models to investigate the effects of single factors/variables on
228 stable hydrogen isotope ratios or C_2, and checked their significance using likelihood ratio tests

against the corresponding null models (i.e. with the variable of interest removed). We also examined the extent to which $\delta^{15}N$ in blood was influenced by age, sex, month, habitats and either $\delta^{2}H$ or C_2 (as indicators of origin), for which general linear models within a Bayesian model averaging (BMA) framework were used. Variables were checked for normality and homogeneity of variance. To avoid over-fitting we tested all combinations of variables, but only included first-order interactions between month, age, sex and study site. Computations were carried out using function bic.glm of BMA package (Raftery et al. 2013), assuming uniform priors for the model parameters and using the Bayesian Information Criterion (BIC) approximation to estimate the integrated model likelihood. We only averaged a subset of all possible models, by constraining the ratio of the posterior probabilities of the candidate model to the best model to be higher than 0.05 (Occam's window criteria Madigan and Raftery 1994). For models including either $\delta^{2}H$ or C_2 we calculated the posterior probability that each variable is in the model (in %), as well as the posterior mean and standard deviation for all estimated coefficients.

RESULTS

Hydrogen isotope trends in Europe

There were highly significant differences in $\delta^{2}H$ values in feathers sampled across a range of different European countries (GLM log-likelihood ratio $\chi^2 = 16499$, $P < 0.001$), with a clear trend for more negative values with increasing distance from Portugal towards north-eastern Europe (Fig. 1). The patterns for the more extensive Portuguese data set are similar, illustrating that even within a smaller region, closer to our winter study sites, latitude of a site and mean $\delta^{2}H$

values of robins from that same location correlate significantly (r = -0.67, N = 16 sites, P = 0.005).

Segregation in winter quarters

As expected there was a correlation between wing pointedness (C_2) and δ^2H in feathers (r = 0.38, N = 121, P < 0.001) for birds captured in central Portugal during winter, indicating that birds with more pointed wings had bred (or were hatched) further northeast. Using the larger data set of birds captured across Iberia, wing length (no data for C_2) also correlated with δ^2H (r = -0.27, N = 170, P < 0.001), again indicating that birds with longer wings originated further northeast.

The δ^2H in feathers did not correlate with latitude of the Iberian wintering site (r = 0.03, N = 174, P = 0.69). Although this analysis is pseudoreplicated (as many individuals came from the same wintering site), we choose to present it as a conservative example of there being no relationship between breeding latitude and wintering latitude. Furthermore, as shown below, there are no reasons to expect important site-related differences in δ^2H composition of feathers of *wintering* robins. The correlation between mean δ^2H in robin feathers from a given wintering site and latitude is also not significant (r = 0.33, N = 5, P = 0.59).

The feathers of robins wintering in open woodland and in shrubland in nearly adjacent sites in central Portugal did not differ significantly in δ^2H (respectively, -87.4 ± 9.6‰, N = 45 and -86.1 ± 12.6‰, N = 77, GLM log-likelihood test χ^2 = 0.002, P=0.997). None of the microhabitat variables measured at Arrábida and at Charneca correlated with stable hydrogen isotope ratios or with the wing pointedness index (all correlations with P > 0.05, N = 45 at Charneca and N = 77 at Arrábida).

Model averaging revealed that values of $\delta^{15}N$ in whole blood differed between habitats, among sampling months and were negatively correlated with $\delta^{2}H$ (Table 1, Fig. 2), while age and sex effects and interactions were non-significant. The same highly significant relationship holds when $\delta^{2}H$ replaces the wing pointedness index C_2 (Table 1, Fig. 2). The percentage contribution of invertebrates in the diet of individual birds (estimated with isotopic mixing models; see Electronic Supplementary Materials for data on Carbon and Nitrogen isotope ratios in prey and robins) showed a negative relationship with $\delta^{2}H$ levels (GLM, t= -2.16 , P=0.034), and also a significant effect of site (GLM, t=14.6, P<0.001).

DISCUSSION

For the first time we have systematically measured variation across multiple niche dimensions amongst sympatrically wintering conspecific migrants from allopatric breeding areas. Perhaps surprisingly we found that robins from a wide range of breeding latitudes within Europe show no evidence of geographic structuring or migratory connectivity within Iberia. Likewise we could find no consistent differences in habitat and microhabitat selection. However, individuals from different origins differed in their trophic position during the winter months, suggesting a form of seasonal matching (Gunnarsson et al. 2005) between the region of birth or reproduction and the wintering ecology of migrants. Trophic specialisation of this nature may play a key role in allowing these populations with different migratory tendencies to co-exist during the non-breeding season.

We began by documenting a clear geographical cline of hydrogen isotope ratios in robin feathers across Europe. The relationship between wing length and shape and $\delta^{2}H$ in wintering birds is also in line with the initial expectation of more negative ratios for birds with longer and

296 more pointed wings, which likely belong to more migratory and northerly distributed populations
297 (Pérez-Tris et al. 2000).

298 The distribution of δ^2H values evidenced in Fig. 1 clearly indicates that the robin
299 communities wintering in our study sites are a mixture of individuals originating from a wide
300 range of latitudes in Europe (a condition necessary for our study) and is in agreement with
301 previous research (Bueno 1998, Catry et al. 2010, Campos et al. 2011a). This panmitic
302 overwintering model at the level of the Iberian Peninsula is similar to that found on
303 overwintering monarch butterflies (Wassenar & Hobson 1998).

304 Many conspecific migrant populations show some segregation in winter quarters, a
305 phenomenon known as migratory connectivity (Newton 2008). Segregation by habitat has more
306 rarely been documented (Marion 1995, Duijns et al. 2009, Alves et al. 2010). In robins, however,
307 we found no habitat influence on the geographical composition of wintering birds, despite the
308 fact that we compared contrasting habitats which, for example, harbour robin communities with
309 markedly different sex-ratios (Catry et al. 2004 and own unpubl. data). A similar result has been
310 obtained for blackcaps, a mostly non-territorial passerine wintering in southern Iberia (de la Hera
311 et al. 2012).

312 Amongst migrants that are territorial during winter, asymmetries in resource-holding
313 potential may result in a despotic distribution, where dominant individuals relegate weaker
314 competitors to less suitable habitats (e.g. Marra 2000). Detailed studies of wintering robins in
315 Iberia have indicated that local birds may have a competitive advantage over visiting migrants,
316 given that they occupy the putative best habitats where they nest throughout the year (Tellería et
317 al. 2001, Tellería & Pérez-Tris 2004). However, the same patterns of population segregation
318 might not necessarily arise from the competitive superiority of southern individuals, but rather

319 from them opting to invest in territorial defence over winter at appropriate sites, in preparation
320 for future breeding attempts. The present study was conducted only at sites where no robins nest.
321 Under these conditions, there was no evidence for habitat separation between birds from
322 different origins, which would be expected if robins from different latitudes had dissimilar
323 abilities to compete for the best wintering sites. Experimental work with artificial feeders also
324 suggested no differences in the resource holding potential linked to geographical origin of robins
325 (Campos et al. 2011b).

326 When potentially competing groups do not segregate in one niche dimension, they are
327 more likely to differ in another one, and this is exactly what we found, with robins from more
328 northerly origins feeding at a higher trophic level (consuming more invertebrates). Wintering
329 robins are broadly omnivorous (Herrera 1977, 1978, 1998, Debusse & Isenmann 1985), which
330 means that any dietary specialization or differentiation is likely to be picked up by an analysis of
331 trophic level given by an indicator such as δ^{15}N in blood. Most robins arrive in October (Bueno
332 1998, Catry et al. 2010), and given the fact that turnover half-life of whole blood for birds the
333 size of a robin is ca. 5 days (Hobson 2008), it is almost impossible that any isotopic
334 measurements made during late-November to February retain any signature of the migratory
335 habitats or of the migratory journey itself.

336 Virtually no studies have documented dietary segregation of coexisting migratory
337 populations in common wintering grounds, and the few exceptions reported very small
338 differences between distinct subspecies (Duijns et al. 2009, Fonteneau et al. 2009). An exception
339 is a study of black-tailed godwits *Limosa limosa* that documented important dietary differences
340 between subspecies, but those were linked to a clear segregation by habitat (Alves et al. 2010). A
341 study of collared flycatchers *Ficedula albicollis* using isotopes also suggested there may be

342 consistent interpopulation differentiation in the feeding ecology at the wintering sites, but
343 alternative explanations for the patterns found could not be rejected (Hjernquist et al. 2009).
344 Individual specialization in diet has been suggested for robins of multiple populations wintering
345 in southern Iberia, which was attributed to differences in morphology, but those were not linked
346 to geographical origin of migrants (Herrera 1978). Our study provides the first strong evidence
347 that different migratory populations may have different diets, even when sharing wintering
348 habitats.

349 Robins from different breeding origins may have slightly divergent adaptations, allowing
350 them to better exploit the resources of their nesting habitats, resulting in an intraspecific niche
351 differentiation (Peterson & Holt 2003). Feeding specializations have been documented in
352 passerine birds even at small spatial scales (10s of kilometres, along an altitudinal gradient) and
353 despite gene flow (e.g. McCormack & Smith 2008). Hence, it seems plausible to speculate that
354 robins originating from different parts of the wide European range could carry different
355 morphological, physiological or behavioural specializations, resulting from local adaptations,
356 into the winter quarters (see Price & Gross 2005, Rayner et al. 2011 for this type of phenomenon
357 amongst closely related migratory species and subspecies). This would then lead them to adopt
358 different diets when sharing a common environment. Such specializations could even be
359 reinforced by selection during winter-time, if they were to reduce competition for resources. An
360 alternative explanation would be that longer-distance migrants have different nutritional
361 requirements than shorter-distance migrant conspecifics (Tellería et al. 2013), but with the
362 present knowledge it is hard to explain why would migrants need a diet richer in protein (from
363 animal prey) and presumably poorer in lipids (Bairlein 2002). It should be noted that muscle-
364 score was not a significant predictor of trophic level, suggesting that body condition or

composition were not strongly correlated with diet. Furthermore, given that differences were present throughout winter, well before spring migratory preparation (fattening) occurs, this alternative explanation seems less likely.

Our findings have implications for models tackling the conditions for the evolution and maintenance of migratory systems. For example, in a theoretical modelling exercise, Taylor & Norris (2007), based on empirical evidence from previous studies (e.g. Adriaensen & Dhondt 1990, Pérez-Tris & Tellería 2002) assumed that migrants experience reduced competitive ability during winter. The results of the present study suggest that (longer-distance) migrants may not necessarily be competitively inferior. Northern robins were not only able to occupy the same habitats as their southern conspecifics despite arriving later to Iberia (Bueno 1998) but they were at a higher trophic level due to a greater consumption of invertebrates. Robins are known to prefer animal to plant foods (Berthold 1976), and so northern individuals may not be faring worse than southern counterparts.

Conclusions

Wintering robins in Iberia have been conclusively shown to clearly segregate between habitats by age, sex and size classes, which has been mostly attributed to the competitive exclusion of weaker individuals from preferred sites by conspecific dominants (Figuerola et al. 2001, Tellería et al. 2001, Catry et al. 2004). The evidence from our work shows that such segregation does not apply to migrants from different regions, suggesting no important asymmetries in the resource holding potential of birds originating from different populations. However, although there are no reported differences in diet between sex and age classes, there is clear evidence for dietary differences between northern and southern individuals. These are perhaps more readily explained

388 by the transportation to the wintering grounds of specializations originating in the breeding areas,
389 but more research is needed to better evaluate the factors underlying these fascinating patterns,
390 and to understand whether this particular type of ecological matching is a frequent trait in
391 migratory species.
392
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407
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570 Table 1. Effects of several predictors on $\delta^{15}N$ levels in blood of robins, using $\delta^{2}H$ (a) and C2 (b)
571 as proxy for geographic origin, estimated by Bayesian model averaging. Values represent
572 posterior probability of each variable has a non-zero coefficient in the model (PP), averaged
573 coefficients (conditional on the variable being in the model) and corresponding standard
574 deviation. Variables with high relevance are represented in bold.
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(a) Seventeen models averaged, the best 5 of which account for a cumulative probability of 0.67	**Posterior Probability (PP)**	**Averaged Coefficients**	**SD of averaged coefficients**
Intercept	**100**	**2.115**	**1.049**
Site (habitat)	**100**	**1.532**	**0.209**
Age	11.5	-0.215	0.235
Sex	7.5	-0.161	0.224
$\delta^{2}H$	**83.2**	**-0.023**	**0.009**
Month (February)	**100**	**-0.648**	**0.866**
Month (After February)	**100**	**0.654**	**1.043**
Muscle	8.1	-0.136	0.201
Month*Site	0	0.000	0.000
Month*Age	0	0.000	0.000
Month*Sex	0	0.000	0.000
Site*Age	5.7	-0.088	0.333
Site*Sex	7.6	-0.319	0.435

Age*Sex	31.4	0.438	0.259

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(b) Seven models averaged, the best 5 of which account for a cumulative probability of 0.67	**Posterior Probability**	**Averaged Coefficients**	**SD of averaged coefficients**
Intercept	**100**	**8.310**	**1.274**
Site (habitat)	**100**	**1.371**	**0.201**
Age	7.1	-0.106	0.201
Sex	7	-0.101	0.201
C2	**100**	**-2.495**	**0.690**
Month (February)	**100**	**-0.854**	**0.712**
Month (After February)	**100**	**0.490**	**0.714**
Muscle	6.6	0.074	0.208
Month*Site	0	0.000	0.000
Month*Age	0	0.000	0.000
Month*Sex	0	0.000	0.000
Site*Age	6.3	-0.065	0.314
Site*Sex	6.3	-0.050	0.349
Age*Sex	11.7	0.278	0.247

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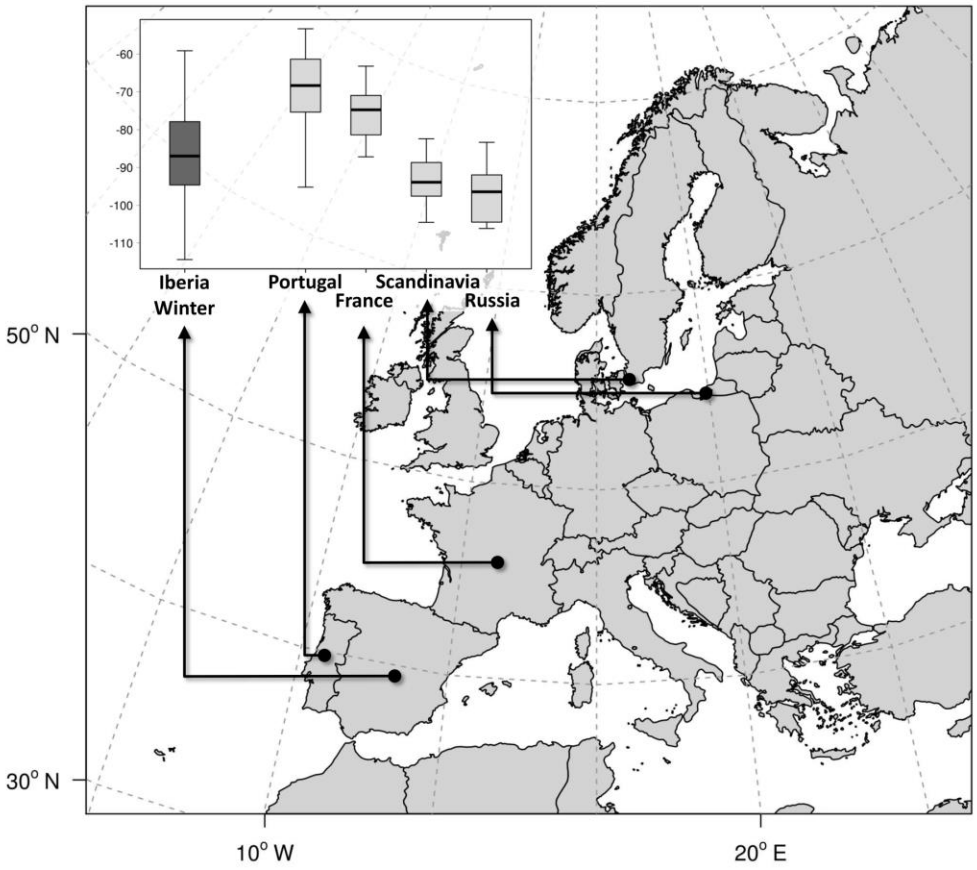
Fig. 1. Box-plot of δ^2H values of robins sampled during the breeding season in Portugal (N=69), France (N = 20), Scandinavia (N = 36) and Kaliningrad enclave, Russia (N = 7) and in winter in Iberia (n=170).

Fig 2. Relationship between (A) δ^2H in feathers (grown in spring/summer) or (B) wing-pointedness index (C_2), and δ^{15}N in whole blood of wintering robins. See Table 1 for statistics.

587 **Fig. 1**



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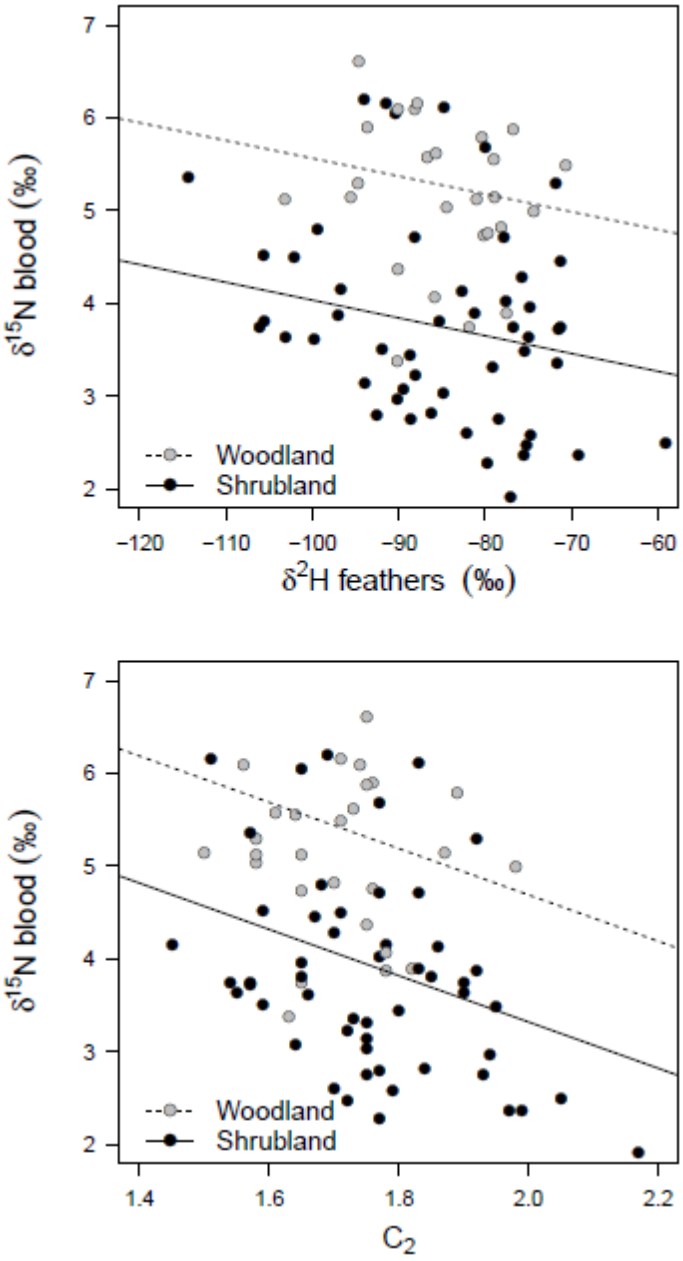
590 **Fig. 2**



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